

1. R. McNeill Alexander presents a simple model for the optimal amount of territory for a bird to try to maintain. Let A be the area of the territory and let p be the daily food availability per unit area, so that the total amount of food available per day is pA . If k is the amount of time (in days) per unit area needed to defend the territory, then $(1 - kA)$ is the amount of time (in days) available for collecting food. Assuming that the bird can collect food at the rate of q units per day, then the amount that can be collected in the time not spent defending the territory is $q(1 - kA)$. The optimal territory is that which has just enough food available so that the bird can collect all of it.
 - (a) Determine the optimal territory size in terms of the various parameters in the model.
 - (b) Let $Q = q/p$. Use this new quantity to obtain a formula for optimal territory size that depends on just two parameters.
 - (c) What is the biological meaning of the parameter Q ? [Hint: look at the units].
 - (d) Suppose $k = 1$. This means that $A = 1$ represents the largest territory that can be defended. We can then interpret a specific value of A as the fraction of defensible territory that the bird should choose. Plot the optimal territory size as a function of the parameter Q .
 - (e) Interpret the graph biologically.
2. Under a given set of assumptions, we can obtain the model

$$r = \log(n)/a$$

for the fractional yearly population growth (i.e., $r = 0.01$ corresponds to a growth rate of 1% per year) as a function of the average number of children per adult (n) and the average age of the mother when a child is born (a).

- (a) Plot r as a function of n over the reasonable range $0.5 \leq n \leq 2$, with a values of 25, 30, and 35. These three curves should be plotted together on one set of axes. Use this figure to discuss the dependence of growth rate on number of children, focusing on how this dependence changes for different average reproduction ages.
 - (b) Plot r as a function of a over the reasonable range $25 \leq a \leq 35$, with n values of 1, 1.5, and 2. These three curves should be plotted together on one set of axes. Use this figure to discuss the dependence of growth rate on average reproductive age, focusing on how this dependence changes for different average numbers of children.
3. Consider a species that has a constant death rate of m individuals per capita per time unit.
 - (a) Given a constant per capita death rate, survival of individuals in a cohort born at the same time is mathematically identical to maintenance of a drug in a patient who gets a single dose at time 0. Use this fact to find a formula for the fraction $y(t)$ of individuals alive at age t . In particular, find the fraction s of individuals alive at age 1 as a function of m .

- (b) Suppose individuals of our hypothetical species mature at age 1 and reproduce at constant rate n until age 2. It can be shown that the birth rate necessary for the overall population to stay at the same size is

$$n = \frac{m}{e^{-m} - e^{-2m}}.$$

Combine this formula with the result of part (3a) to obtain an equation that determines the birth rate necessary for population maintenance as a function of the probability of surviving to maturity.

- (c) Plot the resulting function $n(s)$. Choose a biologically reasonable range of s values for the plot. Discuss the biological significance of the result by comparing the birth rate requirements for animal species with different probabilities of survival to maturity.
- (d) Use a sequence of s values that rapidly approaches 1 to conjecture the value of

$$\lim_{s \rightarrow 1^-} n(s).$$

4. Influenza is an example of a disease that exists in multiple strains with frequent mutations. This means that individuals who recover from the disease are immune to the current strain, but not to the next strain to reach the population. Now suppose a new strain reaches a closed population. Under these circumstances, the standard model for such diseases can be used to predict the fraction d of individuals who contract the disease in terms of the basic reproductive number R_0 , a parameter that represents the average number of secondary infections due to one infected individual in a population of susceptibles. Values of R_0 can vary from 0 to about 20.6 with measles estimated at 12 – 18 and smallpox at 5 – 7. If $R_0 < 1$, then the disease can only infect a few individuals before it dies out. If $R_0 > 1$, then a disease epidemic occurs, and the model predicts that the fraction who get the disease satisfies the equation

$$R_0 d + \log(1 - d) = 0.$$

- (a) Solve the equation for R_0 and use a guess-and-check method to estimate the value of d for $R_0 = 5$. Independent of disease mortality, what does this suggest about the impact of smallpox on a Native American population newly exposed by explorers in the late fifteenth century?
- (b) Plot d as a function of R_0 for the range $0 < R_0 < 5$. (Keep in mind that the given formula is not correct for all values of R_0 . Note that tabular data for two related variables can be plotted with either variable on the horizontal axis.)

5. A resource x is consumed at the rate

$$f(x) = \frac{Ax}{B + x},$$

where A and B are positive parameters.

- (a) What is the maximum consumption rate in terms of A and/or B , achieved in the limit as $x \rightarrow \infty$?
- (b) Suppose the actual consumption rate is half of the maximum from part (5a). What is the corresponding resource level x ?

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Problems. List 2.

6. Consider the family of functions $f(x) = x^4 - 4x^3 - 2bx^2$, where $b > 0$.
- (a) This function has one critical point that does not depend on b . Find and classify this critical point.
 - (b) Factor f' to obtain a quadratic polynomial $q(x)$, with a coefficient that depends on b , whose roots are critical points of f . Are there any requirements that b must satisfy for these critical points to exist?
 - (c) Suppose x^* is one of the critical points satisfying $q(x^*) = 0$. Combine this with the formula for f'' to obtain a formula for $f''(x^*)$ that does not contain b .
 - (d) Use the formula for $f''(x^*)$ from part (6c) to design a test for determining if x^* is a maximum or minimum directly from the value of x^* (so that you won't have to calculate f'' at x^*).
 - (e) Use the test from part (6d) to classify the critical points that satisfy $q(x) = 0$.
 - (f) Suppose you measure a value x_0 with an absolute error of 4%. Use the linear approximation to estimate the maximum relative error of $f(x_0)$.

The problem is more interesting if we analyze all cases for b . We can think of b as a control parameter that we can tune to get a suitable answer of the model (in this case, to control the minimum of the function, for instance). The problem is also very easy if we take into account that, generically, a quartic polynomial with main term x^4 has either 2 minima and 1 maximum in between, or just 1 minimum. By generic, we mean here the cases in which the critical points are nondegenerate (the first derivative vanishes at the critical point, but not the second derivative).

The critical points are the zeroes of $f'(x) = 4x^3 - 12x^2 - 4bx = 4x q(x)$, with $q(x) = x^2 - 3x - b$. The second derivative is $f''(x) = 12x^2 - 24x - 4b$. Then:

- $x_0 = 0$ is a critical point for any b . Since $f''(0) = -4b$, it is a maximum for $b > 0$ and a minimum for $b < 0$. When $b = 0$, the critical point is degenerate, and in fact is an inflection point (notice that $f''(0) = 0$ and $f'''(0) = -24 \neq 0$).
- The other critical points are the zeroes of $q(x)$. If $b > -9/4$ there are two different critical points

$$x_{\pm}(b) = \frac{3 \pm \sqrt{9 + 4b}}{2},$$

if $b = -9/4$ the critical point $x_{\pm}(-9/4) = 3/2$, is degenerate (in fact an inflection point), and no other critical points do exist for $b < -9/4$. In the notation, we have emphasized the dependence of the zeroes on the parameter b .

We finally classify the critical points $x_{\pm}(b)$ for $b > -9/4$.

- If $b > 0$, $x_{-}(b) < 0 < x_{+}(b)$ and, since 0 is a maximum, then both $x_{-}(b)$ and $x_{+}(b)$ are maxima.
- If $-9/4 < b < 0$, then $0 < x_{-}(b) < x_{+}(b)$ and, since 0 is a minimum, then $x_{-}(b)$ is a maximum and $x_{+}(b)$ is a minimum.

The parameter values $b_0 = -9/4$ and $b_1 = 0$ are bifurcations, in which the properties of the model (in this case the number of critical points or their classification) vary. All the information about the problem can be encoded in a bifurcation diagram, a plot on the $b - x$ plane indicating, for each b , the critical points 0 , $x_{\pm}$, and their characteristics. If you plot in the plane $b - x$ the line $x = 0$ and the curve $x^2 - 3x - b = 0$, you will easily obtain the bifurcation diagram of the problem.

Bifurcations at b_0 and b_1 are quite different, and mathematicians like to classify them. At $b_0 = -9/4$ two critical points are born (one minimum and one maximum for $b_0 \gtrsim -9/4$), and the bifurcation is referred to as *fold bifurcation* or *saddle-node bifurcation*. At $b_1 = 0$ two critical points interchange their extremal character, and the bifurcation is a *transcritical bifurcation*.

Notice that we have performed a synthetic study of the problem, rather than analytic as proposed in parts (6c), (6d), and (6e). In this analytic line, since $q(x_{\pm}) = 0$, that is $b = x_{\pm}^2 - 3x_{\pm}$, then

$$f''(x_{\pm}) = 4(3x_{\pm}^2 - 6x_{\pm} - b) = 4(2x_{\pm}^2 - 3x_{\pm}) = 4x_{\pm}(2x_{\pm} - 3).$$

Then:

- If $b > 0$, $x_{-}(b) < 0 < \frac{3}{2} < x_{+}(b)$, then $f''(x_{-}) > 0$ and $f''(x_{+}) > 0$, and both $x_{\pm}$ are minima.
- If $-9/4 < b < 0$, then $0 < x_{-}(b) < \frac{3}{2} < x_{+}(b)$, then $f''(x_{-}) < 0$ and $f''(x_{+}) > 0$, and x_{-} is a maximum and x_{+} is a minimum.

The last outsider question (6f) is just to recall that the derivative let us to estimate the propagation of an uncertainty (error in a variable). In general, if a value x is given by a certain absolute error ε , one writes $x = \bar{x} \pm \varepsilon$. Then

$$f(x) = f(x \pm \varepsilon) \simeq f(x) \pm f'(x)\varepsilon.$$

That is, the absolute value of $f(x)$ is approximately $|f'(x)|\varepsilon$.

7. The marginal value theorem (see Slides Lecture 2) determines the optimal time at which to move to a new patch. A more useful result would be the optimal level of remaining resources. We explore this issue in this problem. Let $f(t)$ be the net amount of resources collected at time t and let $x(t)$ be the size of the patch at time t . Assume that the patch is initially of unit size and that the initial resource deficit is an amount D ; that is, $f(0) = -D$, with $D < 1$.

- (a) Suppose the rate at which the forager obtains resources from a patch is proportional to the resource level of the patch; that is,

$$\frac{dx}{dt} = -kx, \quad k > 0,$$

where the parameter k represents the feeding rate of the forager. Use this equation, along with the information about the initial size, to determine the resource amount $x(t)$.

The equation $\frac{dx}{dt} = -kx$, is a differential equation, whose solution has been found previously in the course: $x(t) = x_0 \exp(-kt)$, where $x_0 = x(0)$. In this case, we are told that the patch is initially of unit size, so $x_0 = 1$. Then, the resource amount at a time t is given by $x(t) = \exp(-kt)$.

- (b) Explain why the quantity $f(t) + x(t)$ should be constant. Use this fact, the initial data, and the answer to part (7a) to obtain a formula for $f(t)$.

Clearly, resources eliminated from the patch because they are collected. Then, $f(t) + x(t)$ must be constant. On the other hand, at time $t = 0$, we know that $x(0) = 1$ and $f(0) = -D$. Therefore, it holds that $f(t) + x(t) = 1 - D$. In particular,

$$f(t) = 1 - D - x(t) = 1 - D - \exp(-kt).$$

- (c) Apply the marginal value theorem to the function f from part (7b) to determine an equation relating the optimal time t^* and the parameters k and D . You will not be able to solve this equation by hand.

We have to maximize $f(t)/t$, that is, the amount collected relative to the time spent. We know that this maximum has to be attained at a point t^* such that $f'(t^*) = f(t^*)/t^*$. Applying this to our particular function, we get that t^* solves the equation:

$$1 - D - \exp(-kt) - tk \exp(-kt) = 0. \quad (1)$$

As we can appreciate, it is not solvable explicitly, so we should proceed numerically (for instance, with the Newton-Raphson method)... provided we knew the numerical values of parameters D and k .

- (d) Use the result of part (7a) to eliminate t^* from the equation of part (7c). The result should be an equation that has only x^* and D .

We must take into account that $x^* = \exp(-kt^*)$ or, equivalently, $t^* = -\frac{1}{k} \log(x^*)$. Substituting these expressions conveniently into (1), we get

$$1 - D - x^* + x^* \log(x^*) = 0. \quad (2)$$

- (e) Plot the optimal residual resource amount x^* against D , using the result of part (7d). Note that the equation does not need to be solved for x^* . Given any x^* between 0 and 1, you can calculate the corresponding value of D and plot the point in the Dx^* plane.

From (2), we can solve for D as $D = 1 - x^* + x^* \log(x^*)$. The function $D(x) := 1 - x + x \log(x)$ is strictly decreasing in the interval $]0, 1[$ since $D'(x) = \log(x)$, and $\lim_{x \rightarrow 0^+} D(x) = 1$ and $\lim_{x \rightarrow 1} D(x) = 0$. Then, as a consequence of Bolzano's theorem and the fact that D is strictly decreasing, for any $D \in]0, 1[$ there exists a unique solution $x^* \in]0, 1[$ of the equation $D = 1 - x + x \log(x)$, that we refer to as

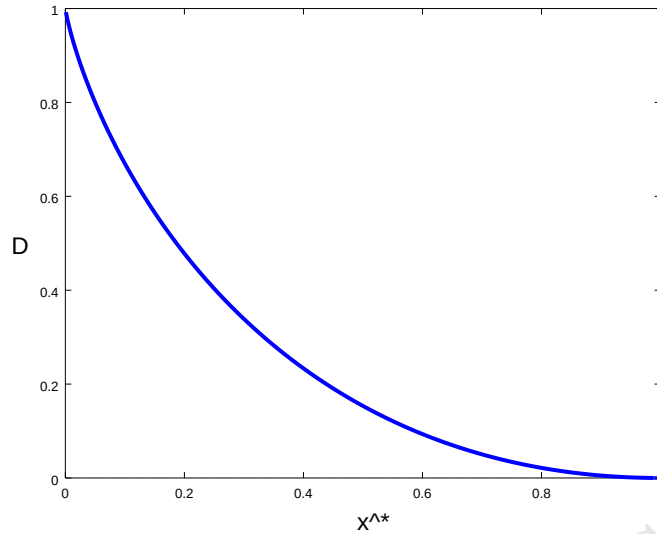


Figure 1: Graph of function $D = 1 - x^* + x^* \log(x^*)$, see Problem 7e.

$x^* = x^*(D)$. The plot for $x^* \in [0, 1[$ is given in Figure 1. The graph of the function $x^*(D)$ is the symmetric one with respect to the line $x^* = D$.

- (f) Interpret the graph of part (7e), noting that D is the cost of travel between patches and x^* is the optimal amount of resource left at the time the forager moves to a new patch. Your discussion should note whether x^* increases or decreases with D and explain this result. It should also address the issues of how large D can be, what happens in the limit as D tends to 0, and what resource deficit amounts correspond to the limiting values $x^* = 0$ and $x^* = 1$.

We recall that x^* is the optimal size of the patch and that the resource deficit is D . The resource deficit can be also interpreted as the energy cost to go from one patch to another. The graph in Figure 1 shows that a “low-cost trip” strategy ($D = 0$) is linked to the decision to leave the patch (optimal time) when it is full ($x^* = 1$), so the strategy of this forager consists of picking a minimum amount from each patch and keeping travelling from one patch to another. Conversely, when $D \rightarrow 1^-$, we see that $x^* \rightarrow 0^+$. That is when moving from one patch to the other is highly expensive, then the strategy of the forager consisting of emptying each patch (leave 0 resources) and move to the following one.

- (g) The final result does not include the rate parameter k . Explain why it is reasonable that the relationship of x^* and D should not depend on k .

The relationship of x^* and D deals with optimal resource levels to leave the patch in terms of the difficulty of moving from one patch to the others. It is coherent, then, that this does not depend on the feeding rate of the forager. However, note that t^* depends on k since this parameter affects directly the time spend to reach the optimal resource level.

8. In a well-known optimal foraging paper, R. Zach reported data on the foraging behavior

of crows. The crows break whelk shells by carrying them above a rocky area and then dropping them onto the rocks. Zach measured the probability of a shell breaking in a fall from a height of x meters and observed that the crows consistently dropped the whelks from a height of approximately 5.25 m. He explained these results as the solution of an optimal foraging problem. Zach did not use calculus to solve the problem, but we will do so in this problem.

It seems reasonable that the optimal strategy for the crows would be to minimize the product of the height and the average number of drops required for the shell to break. This assumption is based on the fact that the energy the crow expends on an upward flight is proportional to the total height. The product of the height per attempt and the number of attempts therefore represents the total energy cost of breaking a shell. Note, however, that the average number of drops required should be a function of the height of the drop. Thus, the function to be minimized is

$$f(x) = x n(x),$$

where we need a model for the function $n(x)$.

- (a) What properties should we expect a graph of $n(x)$ to have? Think in terms of slopes and limiting values.
- (b) Joe Mahaffy has proposed the model

$$n(x) = 1 + \frac{a}{x - b}$$

for the average number of drops needed to break a shell falling from a height of x . Mahaffy found the estimates $a \approx 16$ and $b \approx 1.2$ using Zach's data for shell breaking experiments. Plot the functions $n(x)$ and $f(x)$ with these parameter values. Your plot should only cover the range of x values that make sense (What happens if $x = 1$, for example?). What happens physically if x is outside of the reasonable range? Does Mahaffy's model have the right properties?

- (c) Determine the optimal dropping height for Mahaffy's model with the parameter values he obtained from Zach's data. How does the answer compare with what Zach observed? Does this answer support the model?
- (d) Determine the optimal dropping height for unspecified parameter values.
- (e) Suppose $b = 1.2$. Plot the optimal dropping height as a function of the parameter a .
- (f) Does a larger value of a indicate a harder surface or a softer one? How do you know?

We will do here the parametric analysis. The answers to particular values and plots are left to you.

The function $n(x)$ should (idealistically) satisfy the following properties:

- larger is the height, smaller is the number of drops to broke the shell;
- it should indicate that there are short distances for which never the shell will break;
- for large distances, the shell is broken the first time is drop.

In mathematical terms:

- n is strictly decreasing;
- the domain of n is $]b, +\infty[$ for a certain $b > 0$;
- $\lim_{x \rightarrow +\infty} n(x) = 1$.

Notice that the properties imply that $\lim_{x \rightarrow b^-} n(x) \in]1, +\infty]$.

In particular, Mahaffy's model considers

$$n(x) = 1 + \frac{a}{x - b},$$

where $a, b > 0$ are parameters. This function satisfies the desired properties, and $\lim_{x \rightarrow b^-} n(x) = +\infty$. Since the only critical point of $f(x) = x n(x)$ at the domain $]b, +\infty[$ is $x_*(a, b) = b + \sqrt{ab}$, and $\lim_{x \rightarrow b^-} f(x) = +\infty$ and $\lim_{x \rightarrow +\infty} f(x) = +\infty$, then such a critical point is the absolute minimum of $n(x)$ (at $]b, +\infty[$). Notice that both functions $x_*(a, b)$ and $n_*(a, b)$ are increasing with respect to a .

$x_*(a, b) = b + \sqrt{ab}$ is the optimal dropping height, and the corresponding average of drops is $n_*(a, b) = n(x_*(a, b)) = 1 + \sqrt{\frac{a}{b}}$.

9. The male fiddler crab *Uca pugnax*¹ grows one oversize claw whose only purpose appears to be attracting a mate. The relationship between the claw mass C and the body mass B (not counting the claw mass), both given in milligrams, has been reported to be

$$C = 0.036 B^{1.356}.$$

- (a) Find a formula to relate the growth rates of the claw mass and body mass.

The model is of the form $C = \alpha B^\gamma$, where $\alpha > 0, \gamma > 1$ (in the problem, $\alpha = 0.036, \gamma = 1.356$). Then:

$$\dot{C} = \alpha \gamma B^{\gamma-1} \dot{B}.$$

Equivalently:

$$\frac{d}{dt}(\log C) = \gamma \frac{d}{dt}(\log B).$$

- (b) Plot the ratio of the claw mass growth rate to the body mass growth rate, as a function of the body mass size in grams. Assume the body mass can be as large as 40 g.

The ratio is the function

$$R = \frac{\dot{C}}{\dot{B}} = \alpha \gamma B^{\gamma-1}.$$

It is an increasing function $R = R(B)$, with $R(0) = 0$ and $R'(0^+) = +\infty$. Plot yourself R and [Octave](#) or [WolframAlpha](#) to confirm the results.

- (c) For what body mass size in grams is the growth rate of the claw as large as the growth rate of the body mass?

¹Cranc violinista.

This is when $R = 1$, so

$$B = \left(\frac{1}{\alpha\gamma} \right)^{\frac{1}{\gamma-1}}.$$

For the data, $B \simeq 4.828$ g.

- (d) At what body mass size in grams is the mass of the claw equal to the mass of the body?

This is when $C = B$, so

$$B = \left(\frac{1}{\alpha} \right)^{\frac{1}{\gamma-1}}.$$

For the data, $B \simeq 11.358$ g.

- (e) Assume that the density of body tissues is roughly 1 mg per mm^3 of volume, that the largest dimension of the claw is about 44 mm, and that the body mass is 30 g. Use this information to estimate the shape factor in the length-volume relationship ($V = cx^3$) for a large male claw.

The shape factor is the constant c in the scaling relation $V = cx^3$. Let $\rho = \frac{B}{V}$ be the density of body tissues. Then:

$$c = \frac{V}{x^3} = \frac{B}{\rho x^3}$$

By substitution of the data, we get $c \simeq 0.352$.

10. The focal length of the lens in the human eye adapts to the distance of the object being viewed. The necessary length is given approximately by the thin lens formula

$$\frac{1}{f} = \frac{1}{x} + \frac{1}{v},$$

where f is the focal length of the lens, x is the distance of the object, and v is a positive constant. [The lens has a maximum focal length f_0 ; muscles in the eye automatically decrease the focal length when viewing nearby objects.]

- (a) What is the physical significance of the parameter v ? [Hint: Find a value of x for which the relationship between f and v is particularly simple.]

The parameter v is determined by the focal power of the cornea and the distance from the lens to the retina. A geometrical way to see the relation among f , x and v is through the schema of Figure 2. The thin lens formula can be proved using this construction (for instance, computing the intersection of the two dashed lines: one joining the tip of the object with the center of the lens, and the other from the projection of the tip of the object on the lens, all the way through the focus of the lens).

- (b) Suppose an object is approaching you at a speed of 10 miles per hour (16.1 km/h, or 4.47 m/s). How rapidly must your eye's focal length change when the distance of the object is 30 m? What about 10 m? You may assume $v = 17$ mm.

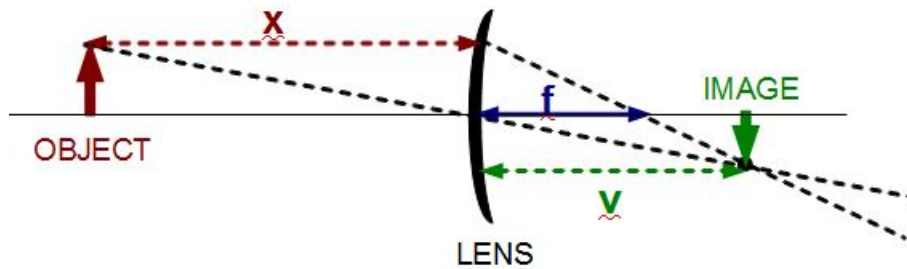


Figure 2: Schematic representation of focal value, distance to the object and distance to the image, see Problem 10a.

Since the object is moving, we have to assume that $x = x(t)$. Accordingly,

$$\frac{1}{f(t)} = \frac{1}{x(t)} + \frac{1}{v}.$$

We want to know the rate the focal length changes, $f'(t)$, from two data: $x'(t) = 4.47$ m/s and $x(t) = 30$ m. The results will be given with three significant digits, that is, rounding to the third digit after the last 0 from the left. We assume also that $v = 17$ mm. Then, at this point

$$\frac{1}{f} = \frac{1}{30} + \frac{1}{0.017} \Rightarrow f \approx 0.0170 \text{ m} = 17.0 \text{ mm}.$$

To relate these quantities the rates of change, we must derive the above equation with respect to t :

$$\frac{-f'(t)}{f(t)^2} = \frac{-x'(t)}{x(t)^2} \Rightarrow f'(t) = \frac{x'(t) f(t)^2}{x(t)^2} \Rightarrow f'(t) \approx \frac{4.47 \cdot 0.0170^2}{30^2} \approx 0.00143 \text{ mm/s}.$$

When $x(t) = 10$ m, then we obtain $f \approx 17.0$ mm and $f'(t) \approx 0.0129$ mm/s.

As an extra challenge, you can try to provide a formula for $f'(t)$ valid for any distance x , as a function of the velocity v_0 .

11. Suppose the number of prey animals eaten per predator per day is given by

$$y = \frac{x}{1 + hx}, \quad h > 0,$$

where x is the number of prey animals per unit area.

- (a) Determine the rate at which predation is changing with respect to time in terms of the quantities $x(t)$ and $x'(t)$.

We have to assume that both $x(t)$ and $y(t)$ change with time. Thus, $y(t) = \frac{x(t)}{1 + hx(t)}$ and so,

$$y'(t) = \frac{x'(t)(1 + hx(t)) - x(t)hx'(t)}{(1 + hx(t))^2} = \frac{x'(t)}{(1 + hx(t))^2}.$$

- (b) Suppose the prey population is growing at the rate rx , where $r > 0$. Use this additional information to determine the rate at which predation is changing with respect to time in terms of $x(t)$ alone.

The variation of the prey population can be written as $x'(t) = rx(t)$. Then, we can substitute into the previous relation:

$$y'(t) = \frac{rx(t)}{(1 + hx(t))^2}.$$

12. Suppose the biomass $x(t)$ of a plant changes according to the differential equation

$$\frac{dx}{dt} = rx - \frac{qx}{a+x}, \quad a, q, r > 0,$$

where the first term represents plant growth and the second represents herbivory. Define new variables X and T and parameter q by $X = x/a$, $T = rt$, and $Q = q/(ra)$.

- (a) Use the chain rule to obtain a differential equation for $X(T)$. [Hint: You can work with more than two factors, which is necessary here since you have a derivative formula for dx/dt along with algebraic relations between x and X and between t and T . Note that you must also use the algebraic formula to replace x by X ; your result should have no lowercase symbols.]
- (b) Note that X and T represent the plant biomass and time. If we want to study the effect of growth and herbivory on plant biomass, why might we prefer to study $X(T)$ rather than $x(t)$?

We will apply the chain's rule taking into account that X depends linearly on x , x depends on t (the differential equation is about this dependence), and t depends linearly on T .

$$\begin{aligned} \frac{dX}{dT} &= \frac{dX}{dx} \frac{dx}{dt} \frac{dt}{dT} = \frac{1}{a} \left(rx - \frac{qx}{a+x} \right) \frac{1}{r} \\ &= \frac{1}{ar} \left(raX - \frac{qaX}{a+aX} \right) = X - \frac{QX}{1+X}. \end{aligned}$$

Notice that these changes of variables and parameters allow a simpler relation, that depends on a single parameter, Q .

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Problems. List 3. Taylor expansions.

15. Consider the function $f(x) = e^x \cos x$.
- (a) Find the corresponding second order Taylor polynomial, $P_2(x)$, around $x_0 = 0$.
 - (b) Use $P_2(0.5)$ to approximate $f(0.5)$. Find an error bound for $|f(0.5) - P_2(0.5)|$ using the error formula and compare it with the actual error.
 - (c) Find an error bound for $|f(x) - P_2(x)|$ for $x \in [0, 1]$.
 - (d) Compute the power series of the function f and determine the corresponding interval of convergence.
 - (e) How many terms should we add to compute $f(0.5)$ with a maximum error of 10^{-8} ?
16. Find the power series of the following functions and determine the corresponding interval of convergence.
- (a) $f(x) = \frac{x}{1 - x^2}$;
 - (b) $f(x) = e^{x^3 - 1}$;
 - (c) $f(x) = x^2 \sin x$;
 - (d) $f(x) = e^x \ln(1 + x) + \cos x$.
17. Consider the function $f(x) = \arctan x$.
- a) Compute the series of $f(x)$. Hint: $f'(x) = \frac{1}{1 + x^2}$.
 - b) Considering that $\arctan(1) = \pi/4$, find a numerical series to compute π .
 - c) What can you obtain by considering $\arctan(1/\sqrt{3}) = \pi/6$ instead of $\arctan 1$?
18. The state equation of a certain gas follows the *Dieterici's equation*:

$$P(V - nb) = nRTe^{-an/RTV}.$$

Find the first terms of the corresponding virial series. Compute the Boyle's temperature in terms of a and b (see the notes around the Van der Waals model given in Lecture05.)

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Problems. List 4.

17. Practice the concept of integral in the following questions:

- (a) A runner's respiration rate during a 30-min training run is $r(t)$ breaths per minute. Construct an integral to calculate the total number of breaths over the course of the run.
- (b) Suppose $t = \int_0^Y f(y) dy$ represents the time required for Y grams of a toxin to be eliminated from an organism's bloodstream. What does $f(y)$ represent? In particular, what does $f(Y/2)$ represent?
- (c) The population density of a plant species is $f(x)$ individuals per square meter, where x is the distance from a river, with $f(x) \geq 0$ for $x \leq 100$ and $f(x) = 0$ for $x \geq 100$. Construct an integral to calculate the number of plants along a section of river of length L .
- (d) The population density of a plant species is $f(r)$ individuals per square meter, where r is the distance from the center of a circular lake of radius 100m. Assume the density falls to 0 at a distance of 100m from the lake. Construct an integral to calculate the total number of plants.

18. Write the sum $S(k) := \int_{-1}^0 (1+x)e^{-kx} dx + \int_0^1 (1-x)e^{-kx} dx$, where $k \neq 0$, as a single integral by the change of variables $y = 1+x$ in the first integral. Compute $S(k)$.

19. Consider the function $f(x) = \frac{1}{\sqrt{1-x^2}}$.

- (a) Plot $f(x)$ on the interval $0 \leq x < 1$. Can you tell from the graph whether the area under this curve is finite?
- (b) Use the table of basic primitives to compute $g(b) = \int_0^b f(x) dx$ for $0 \leq b \leq 1$.
- (c) Plot the function $g(b)$ defined in (19b).
- (d) What is $\int_0^1 f(x) dx$?

20. In Lecture 6 we have studied the *area under the (glucose) curve* (AUC) as a measure to diagnose gestational diabetes. In particular, we have shown that experimental data have a good fit with functions of type $y(t) = (a + bt) \exp(-ct)$, where $a, b, c > 0$, t is the time in minutes and y is the level of glucose in mmol/l.

- (a) Give a general formula for the AUC $\int_0^{120} y(t) dt$ in terms of parameters a , b and c . Using the values $a = 4.0014$, $b = 0.20549$ and $c = 0.018858$, obtain the result given in Slide 7 of Lecture 6. What is the average level of glucose of this subject?

- (b) Show that the average level of glucose tends to zero if we increase the time interval indefinitely. Hint: use that $\int_0^{+\infty} y(t) dt := \lim_{M \rightarrow \infty} \int_0^M y(t) dt$ is finite.

Numerical integration

21. Compute a power series expansion of $\int_0^2 \sin(x^2) dx$. How many terms do we need to sum in order to get an error smaller than 10^{-6} .
22. The error in computing numerically a definite integral by using the trapezoidal rule with step h is approximately proportional to h^2 . In fact, it can be proved the following asymptotic formula:

$$\lim_{h \rightarrow 0^+} \frac{I(f) - I_T(f, h)}{h^2} = C,$$

where $C = C_T(f)$ is a constant that depends on f (in fact, on its second derivative). Hence: $I(f) \simeq I_T(f, h) + C h^2$.

- Applying the trapezoidal rule with steps $2h$ and h , obtain an approximation of the asymptotic constant C , and of the error $I(f) - I_T(f, h)$.
 - From the previous approximation, guess how many steps n we would need to compute the integral with an error smaller than a given tolerance ε ?
 - Apply the results to the example $\int_0^2 \sin(x^2) dx$, explained in Lecture 6, and guess the number of steps for getting an error smaller than 10^{-6} .
- Note: You can make some of the computations by hand, but in order to analyze all results in the table of results, you may use a spreadsheet, such as **Excel** or **LibreOffice**.
23. The asymptotic expansion of the error in the approximation of a definite integral by using the trapezoidal rule is of the form

$$I(f) - I_T(f, h) = C_2 h^2 + C_4 h^4 + C_6 h^6 + \dots$$

- Show that, by applying the trapezoidal rule with steps h and $h/2$, we can eliminate $C_1 h^2$ in the previous formula and get a new approximation of $I(f)$ whose error is approximately proportional to h^4 .
- Show that, if we have applied the trapezoidal rule with steps h , $h/2$ and $h/4$, we can repeat the previous argument and get an approximation whose error is approximately proportional to h^6 . Notice that we could repeat the procedure if we had more initial approximations.
- Apply the results to the example $\int_0^2 \sin(x^2) dx$, explained in Lecture 6.

Hint: Read the **Wikipedia** entries for *Richardson's extrapolation* and *Romberg's method*.

24. Adapt the two previous exercises to Simpson's method, having into account that the asymptotic expansion of the error is, in this case, of the form

$$I(f) - I_S(f, h) = C_4 h^4 + C_6 h^6 + \dots$$

25. Apply all the previous methodologies and results to compute $\int_0^1 \frac{\sin x}{x} dx$.

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Problems. List 5.

26. Study the bifurcations of equilibria and plot the bifurcation curves in terms of the parameter r in the following cases:

- (a) $\dot{x} = r x - x^2$ (*transcritical bifurcation* at $r = 0$).
- (b) $\dot{x} = r + x^2$ (*saddle-node bifurcation* at $r = 0$).
- (c) $\dot{x} = r x - x^3$ (*pitchfork bifurcation* at $r = 0$).

In each case, determine the stability character of each branch of the bifurcation diagram.

27. In Lecture 07, we have studied the logistic growth model

$$\dot{x} = r x (1 - x/K), \quad r > 0, K > 0,$$

where x stands for the size of a biological population, r is the birth rate and K is the carrying capacity (e.g., due to the competition for food).

- (a) Prove that $x = 0$ and $x = K$ are the only equilibria and determine their stability.
- (b) Consider the logistic growth model with linear harvesting¹ introduced in Lecture 07 which assumes the harvesting to be modelled as $p x$, where $p > 0$ is a parameter:

$$\dot{x} = r x (1 - x/K) - p x, \quad r > 0, K > 0, p > 0. \quad (1)$$

Prove that the population can be preserved if we take $p < r$ and plot (qualitatively) the curve of equilibria versus p , for $p \in [0, 2r]$ (assuming r and K fixed). What does it happen, in biological terms, if $p > r$?

- (c) Match the bifurcation described in (27b) with one of the bifurcations studied in Problem 26.
28. The growth of cancerous tumors can be modeled by the Gompertz law $\dot{N} = -a N \log(b N)$, where $N(t)$ is proportional to the number of cells in the tumor, and $a, b > 0$ are parameters. The predictions of this simple model agree surprisingly well with data on tumor growth, as long as N is not too small.
- (a) Use phase line analysis to determine the stability of the equilibria.
 - (b) Give an explicit solution of the model assuming that $N(0) = e/b$ and show that the corresponding orbit tends to $N = 1/b$.

¹Also known as Schaeffer model, often used to model the impact of harvesting on a fish population.

29. Use phase line analysis to determine the stability of the equilibria for the model

$$\frac{dN}{dt} = -N \left(1 - \frac{N}{T}\right) \left(1 - \frac{N}{K}\right), \quad 0 < T < K,$$

where the parameter K has the same biological meaning that it has in the logistic model. Assuming that N is a population, explain the biological meaning of T .

30. Consider the *integrate and fire model*, introduced in Lecture 07, which is governed by equation

$$C \frac{dv}{dt} = -g_L (v - V_L) + I,$$

under the following rule: if v exceeds a certain value V_{thr} , then v is reset to a lower value V_{reset} . Typically, $V_{thr} \approx -30\text{mV}$ and $V_{reset} \approx -70\text{mV}$, while g_L is the order of 1 and $V_L \approx -65\text{mV}$. In Lecture 07, we proved that $\lim_{t \rightarrow +\infty} v(t) = V_L + I/g_L$. Assuming that $V_L + I/g_L > V_{thr}$, prove that the solution of the differential equation will be periodic with period

$$T = \frac{-C}{g_L} \log \left(\frac{V_{thr} - V_L - I/g_L}{V_{reset} - V_L - I/g_L} \right).$$

31. The θ -model is a 1D model of neuronal dynamics that assumes the angle θ to be the phase along an oscillation. It is written as

$$\frac{d\theta}{dt} = 1 - \cos \theta + (1 + \cos \theta) I, \quad \theta \in [-\pi, \pi] \quad (2)$$

and θ is represented as angle on a circle. Moreover, when $\theta = \pi$, the neuron is supposed to “spike”.

- (a) Plot the function $x = \tan(\theta/2)$ for $\theta \in [-\pi, \pi]$.
 (b) Prove that equation (2) can be brought into equation

$$\frac{dx}{dt} = x^2 + I$$

by means of the change of variables $x = \tan(\theta/2)$. From Problem 26, observe that the model undergoes a saddle-node bifurcation at $I = 0$.

- (c) Consider $I > 0$ and take an initial condition $x(0) = x_0$. Prove that the time to reach the spike can be expressed as

$$T_{spike} = 1/2 \left(-2 \arctan \left(\frac{x(0)}{\sqrt{I}} \right) + \pi \right) \frac{1}{\sqrt{I}}.$$

In particular, if we reset $x(t)$ to $-\infty$ ($\theta = -\pi$) the *total transit time* to reach $+\infty$ ($\theta = \pi$) is

$$T_{per} = \frac{\pi}{\sqrt{I}}.$$